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PHYLOGENY OF *TRICHIA BRUNNEA* AND NEW NAMES IN THE GENUS *ARCYRIA* (*TRICHIALES*, *MYXOMYCETES*)

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Recent phylogenetic studies indicate taxonomic uncertainty of some species in the genera *Arcyria* (*Arcyriaceae*) and *Trichia* (*Trichiaceae*). For example, a phylogenetic position of *Trichia brunnea* still is not resolved. We revised a taxonomic position of this species based on extensively sampled *18S nrDNA* sequences, as well as a morphological analysis of sporocarps and spores. The nomenclatural history of *T. brunnea* is briefly presented and a comprehensive morphological description of the species is provided. In result, we support the transfer of *T. brunnea* to *Arcyria*. Because of the name *Arcyria brunnea* exists already, we propose a new name, *A. brunneo-iridescens* (= *Trichia brunnea*).

Keywords: Amoebozoa, *Arcyria*, distribution, *Myxogastria*, myxomycetes, taxonomy, *Trichia*, *18S nrDNA*

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INTRODUCTION

Arcyria F.H. Wigg. is a widely distributed genus of *Arcyriaceae* with 55 species currently accepted (Lado, 2005–2023). The genus traditionally can be recognized by its capillitium hollow threads, consissiting of cogs, reticula, rings, spines, and verrucae, whereas species of the family *Trichiaceae* have the capillitium ornamented by spirals (Martin, Alexopoulos, 1969). However, the phylogenetic analysis shows that the spiral ornamentation of the capillitium seems to have originated independently in multiple clades of myxomycetes (Fiore-Donno et al., 2013) and most genera of *Trichiales* are paraphyletic (Walker et al., 2015; Leontyev et al., 2019; Ronikier et al., 2020). In the last phylogenetic study of *Trichiales* (García-Cunchillos et al., 2022) proposed taxonomic amendments for some taxa to reflect both the phylogenetic affinities and the evolution of the morphological traits. However, some rare species, for example *Trichia brunnea*, were not studied and a phylogenetic position of this species still is not resolved.

T. brunnea was described by Cox in 1981 from sporangia developed on specimens of weathered cow dung in moist chamber culture and collected in California, United States (Cox, 1981). In addition to the type locality this species known in Austria (Trichia brunnea, 2023a), Denmark (Trichia brunnea, 2023b), Montenegro, Norway (Eliasson et al., 1991), Russia: arid regions of the Lower Volga River Basin (Novozhilov et al., 2006) and Altay Territory, border of the Pre-Altai Plain and the spurs of the northwestern ridges of the Altai Mountains (Vlasenko et al., 2017). We also found *T. brunnea* in 2018 in Altay Territory and in 2020 and 2021 in the Republic of Tyva and the Republic of Sakha (Yakutia). Everywhere this species is rare and sporadically isolated in moist chamber cultures.

To clarify the taxonomical position of *T. brunnea* we used a *18S nrDNA* gene phylogeny as well as detailed morphological description based on light and scanning electron microscopy of our collections.

MATERIALS AND METHODS

Sampling, moist chamber cultures and morphological analyses. The sporocarps of *T. brunnea* for this work were obtained in moist chamber cultures using glass Petri dishes (10 cm diam.) lined with filter paper as described by literature (Gilbert, Martin, 1933; Härkönen, 1977). In this study we used a modified cultivation method (Vlasenko, Vlasenko, 2020); the duration of cultivation of epiphytic species has been increased to 3–6 months. Moist chamber were examined for the presence of myxomycetes under high magnification with a dissecting microscope. The collections upon which the molecular analysis and morphological de-

scription is based were studied with a Carl Zeiss Stemi DV4 stereomicroscope and a Carl Zeiss Axiolab A compound microscope. Scanning electron micrographs were obtained with a Carl Zeiss EVO MA 10 scanning electron microscope (SEM) in CSBG SB RAS. Specimens mounted on aluminum stubs via double-sided sticky film and sputter-coated with gold. The examined specimens have been deposited in the M.G. Popov Herbarium, USU 440537, Novosibirsk (NSK). The nomenclature used corresponds to Lado (2005–2023).

DNA extraction and sequencing. To extract DNA, sporophore fragments were crushed using aluminum oxide (Al_2O_3). Then they were homogenized in a buffer for lysis of Phyto-Sorb kit (Synthol, Moscow). The *18S* (*SSU*) nrDNA regions were amplified with standard primers for bright-spored myxomycetes SFATri and SR4Bright (Fiore-Donno et al., 2013). The HS Taq DNA Polymerase (Evrogen, Moscow) was used. PCR load (50 μL): 35.25 μl PCR-grade water, 5 μl 10X Taq PCR Reaction Buffer (Eurogen, Moscow), 2.5 μl 50 mM $MgCl_2$ (Eurogen, Moscow), 0.5 μl 20 μm each dNTPs (Eurogen, Moscow), 1 μl 10 ng/μl each primer (Biosset, Novosibirsk), 0.75 μl 5 u/μl SNPdetect HS Taq DNA Polymerase (Eurogen, Moscow) and 4 μl 10 ng/μl DNA, adjusted with ddH_2O. PCR cycling conditions were as follows: denaturation for 5 min at 94°C, followed by 36 cycles (15 s at 94°C, 15 s at 50°C, 1 min at 72°C) and a final elongation for 7 min at 72°C. PCR products were sequenced using Big Dye terminator cycle sequence kit (ABI) and ABI Prism 3130 sequencer (Perkin-Elmer, USA) at SB RAS Genomics Core Facilities (ICBFM SB RAS, Novosibirsk, Russia). All the sequences generated in the study are deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank).

Phylogenetic analysis. Sequenograms of *T. brunnea* were analysed in Chromas version 2.6.6 (http://technelysium.com.au/wp/chromas/). We generated the sequences for *T. brunnea* partial *18S* regions of nrDNA (the first *ca*. 580 nucleotides). New sequences were compared with the available data in GenBank using the Nucleotide BLAST tool (Altschul et al., 1990). Based on the BLAST search, was incorporated additional 18S sequences of other related species into the analyses. The final dataset included 57 *18S* sequences, respectively. *Dianema subretisporum* Kowalski, *Dianema depressum* (Lister) Lister, *Tubifera ferruginosa* (Batsch) J.F. Gmel., and *Reticularia lycoperdon* Bull. was used as an outgroup (García-Cunchillos et al., 2022). Table 1 provides an overview of the taxa we used, information on the herbarium specimens, GenBank accession numbers and references. Sequences were aligned online in MAFFT (Katoh et al., 2002), version 7 (Katoh, Sandley, 2013) using the E-INS-I strategy (Katoh, Toh, 2008). MEGA X software (Kumar et al., 2018) was used for statistical analysis of nucleotide datasets. The phylogenetic relationships were reconstructed using the Maximum Likelihood (ML) method (Felsenstein, 1981). Phylogenetic trees were constructed in the online version program of IQ-TREE (Trifinopoulos et al., 2016) of IQ-TREE software (Nguyen et al., 2015). Nonparametric bootstrapping with 1000 replicates as statistical used support in this analysis. The phylogenetic trees were visualized in Fig Tree version 1.4.4 (Rambaut, 2018).

RESULTS

Phylogenetic analysis

A preliminary blast analysis of the *18S* (*SSU*) nrDNA region showed that the sequences of *Trichia brunnea* had the maximum homology with the species of the *Arcyria* genus.

The ML analysis of the *18S nrDNA* gene showed that *Trichia brunnea* is closest to *Arcyodes incarnata* (Alb. et Schwein.) O.F. Cook [= *Arcyria congesta* (Sommerf.) Berk. et Broome]. The genetic distance of the "*Trichia brunnea*" branch on the *SSU* tree is 0.168, with 98% bootstrap support (Fig. 1).

An analysis of the molecular phylogeny of the order *Trichiales* shows that the family *Arcyriaceae* is divided into two groups of species (García-Cunchillos et al., 2022). *Arcyriaceae* s.str. includes the species *Arcyria affinis*, *A. denudata*, *A. imperialis*, *A. incarnata*, *A. minuta*, *A. stipata*.

Our study showed that the clade to which *Trichia brunnea* belongs also includes the species *Arcyodes incarnata* and *Arcyria affinis*. Species *A. denudata* (L.) Wettst. is the type for the genus *Arcyria* Hill ex F.H. Wigg. Thus, *Trichia brunnea* has no phylogenetic relationship with species of the *Trichiaceae* family and belongs to the *Arcyriaceae* family.

In result, we support the transfer of *T. brunnea* to the genus *Arcyria*. The name *Arcyria brunnea* Nann.-Bremek. et Y. Yamam., 1986 has been already used and this name is a synonym of *A. incarnata* (Pers. ex J.F. Gmel.) Pers. (1796) [≡ *A. incarnata* f. *brunnea* (Nann.-Bremek. et Y. Yamam.) Y. Yamam., 1998], so we propose here a new species epithet.

Taxonomy

Arcyria brunneoiridescens A. Vlasenko, Novozh. et V. Vlasenko nom. nov. (Figs 2–4).

MycoBank No: MB849577.

= *Trichia brunnea* J.J. Cox, Mycologia 73 (4): 741, 1981.

Etymology: Refers to the color of the peridium.

Description: Sporangia stalked, sometimes sessile, on a narrowed base, gregarious, often overlap each other, or fused with each other, resulting in the formation of pseudoethalia, individual sporangia oval, ovoid, irregular, brilliant brown, iridescent, 0.3–0.5 mm wide, 0.5–1 mm tall. Stalk thin, straight, curved, rugose, yellow-brown, up to half the total height of sporangium, sometimes short, like a continuation of the hypothallus, olive-brown in transmitted light, always filled with spore-like cells 11.5–20.5 μm diam. Peridium single-

Table 1. The sequences used for the alignment

Species	Herbarium voucher/isolate; GenBank accession numbers; references
Cornuvia serpula	MM29198; JX481285; Fiore-Donno et al. (2013)
Gulielmina megaspora	MA: Fungi: 82123; MT154026; García-Cunchillos et al. (2022)
G. vermicularis	MA80426; ON713363; García-Cunchillos et al. (2022)
Hemitrichia abietina	MA58838; ON713338; García-Cunchillos et al. (2022)
H. calyculata	MA81807; ON713370; García-Cunchillos et al. (2022)
H. clavata	MA62018; ON713344; García-Cunchillos et al. (2022)
H. crassifila	MA: Fungi: 91885; MT154031; Ronikier et al. (2020)
H. decipiens	MA83070; ON713379; García-Cunchillos et al. (2022)
H. intorta	KR0022295; MT154021; Ronikier et al. (2020)
H. lutescens	MA83430; ON713391; García-Cunchillos et al. (2022)
H. minor	MA80197; ON713361; García-Cunchillos et al. (2022)
H. pardina	MA80413; ON71336; García-Cunchillos et al. (2022)
H. serpula	NSK 1031916; ON863805; the current study
" "	NSK 1030527; OP725706; the current study
Metatrichia floriformis	MA83204; ON713382; García-Cunchillos et al. (2022)
M. floripara	Lado25103; ON713324; García-Cunchillos et al. (2022)
M. horrida	MA81778; ON713369; García-Cunchillos et al. (2022)
M. vesparium	MA51719; ON713334; García-Cunchillos et al. (2022)
Oligonema affine	MA78975; ON713357; García-Cunchillos et al. (2022)
O. flavidum	DWM5764; JX481304; Fiore-Donno et al. (2013)
O. favogineum	MA83229; ON713383; García-Cunchillos et al. (2022)
O. persimile	–/AY643826; Fiore-Donno et al. (2005)
O. schweinitzii	MA85559; ON713399; García-Cunchillos et al. (2022)
O. verrucosum	MA83489; ON713394; García-Cunchillos et al. (2022)
Ophiotheca calongei	MA78692; ON713353; García-Cunchillos et al. (2022)
O. chrysosperma	MA63754; ON713345; García-Cunchillos et al. (2022)
O. pedata	MA81941; ON713372; García-Cunchillos et al. (2022)
Perichaena agaves	MA50703; ON713332; García-Cunchillos et al. (2022)
P. corticalis	AMFD157; JX481306; Fiore-Donno et al. (2013)
P. depressa	NSK 1031856; ON863804; the current study
P. dictyonema	MA59057; ON713340; García-Cunchillos et al. (2022)
P. liceoides	M0073211; ON713328; García-Cunchillos et al. (2022)
P. longipes	LMW-2015; KP241120; Walker et al. (2015)
P. luteola	DWM4984; JX481308; Fiore-Donno et al. (2013)
P. nigra	MA86774; ON713402; García-Cunchillos et al. (2022)
P. quadrata	MA88310; ON713407; García-Cunchillos et al. (2022)
P. stipitata	MA79150; ON713358; García-Cunchillos et al. (2022)
Trichia alpina	MA80534; ON713364; García-Cunchillos et al. (2022)
T. brunnea	NSK 1016772; OR287437; the current study
" "	NSK 1030490; OR287438; the current study
" "	NSK 1031862; OR287439; the current study
" "	NSK 1016771; OR287440; the current study
" "	NSK 1016774; OR287441; the current study
" "	NSK 1016773; OR287442; the current study
T. contorta	sc22513; KT358722; Feng, Schnittler (2017)

Table 1. (Contd.)

Species	Herbarium voucher/isolate; GenBank accession numbers; references
T. erecta	sc22424; KT358724; Feng, Schnittler (2017)
T. scabra	MA90224; ON713410; García-Cunchillos et al. (2022)
T. sordida	AMFD 81; EF513182; Fiore-Donno et al. (2010)
T. varia	NSK 1016006; OP725705; the current study
Tubifera ferruginosa	AMFD 196; EF513171; Fiore-Donno et al. (2010)

layered, membranous, translucent, with iridescent tint, with crack lines in the apical part of the sporotheca, after dehiscence remains in the form of a deep cup at the base. In the SEM, the inner surface of the peridium is ornamented with warts, often in groups; the outer surface of the peridium is ornamented with folds and lines. Capillitium olive, light brown, composed of simple or slightly branched elaters of various lengths. Elaters are ornamented with spiral thickenings and warts, about 2–3.5 μm diam., sometimes almost smooth. Elaters

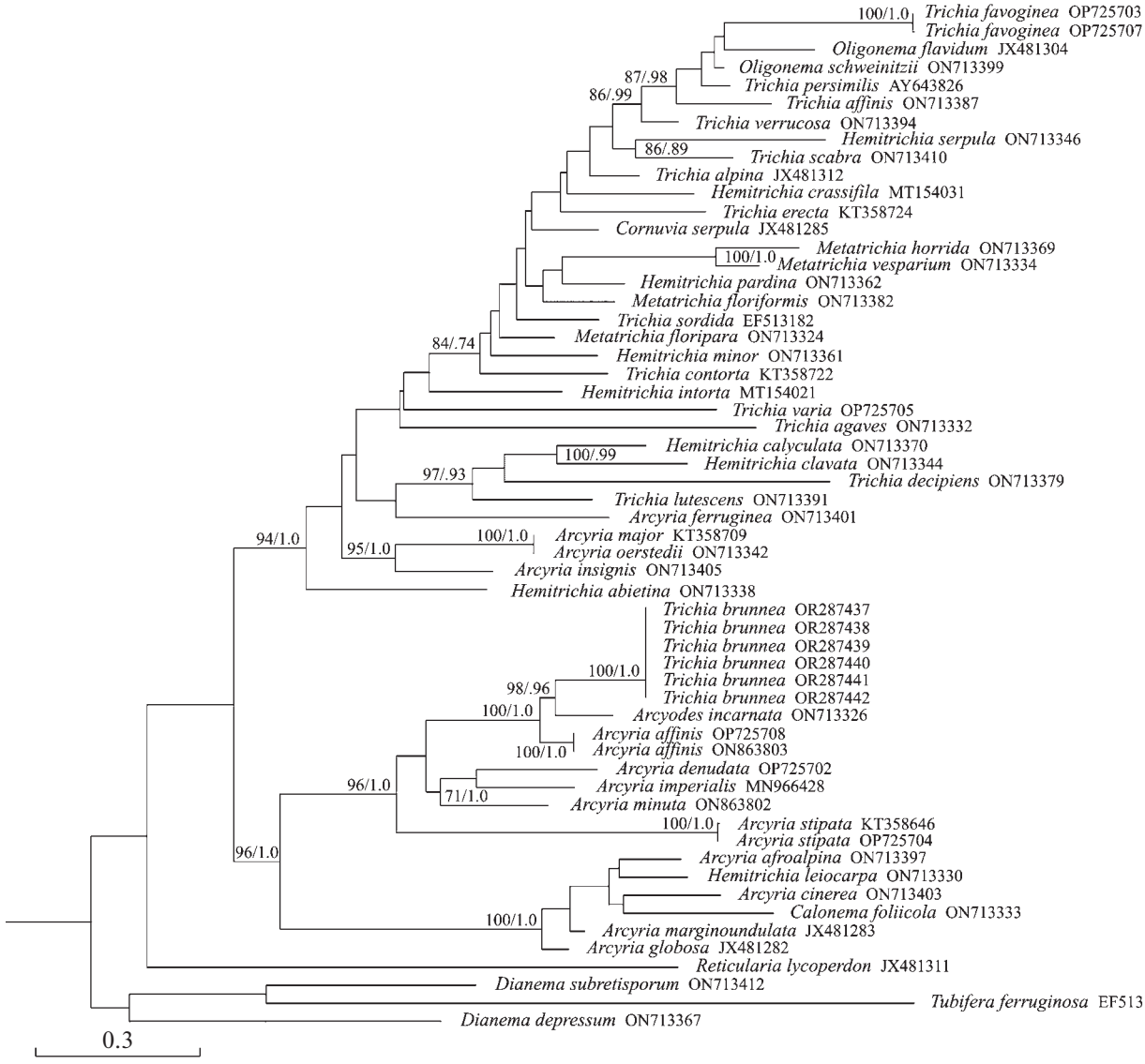

Fig. 1. The maximum likelihood tree based on *18S nrDNA* sequences shows the phylogenetic relationships between the *Trichia brunnea* and other closely related species of bright-spored myxomycetes. BS values with high support and Bayesian posterior probabilities are shown in the branches. GenBank access numbers are given after the species name.

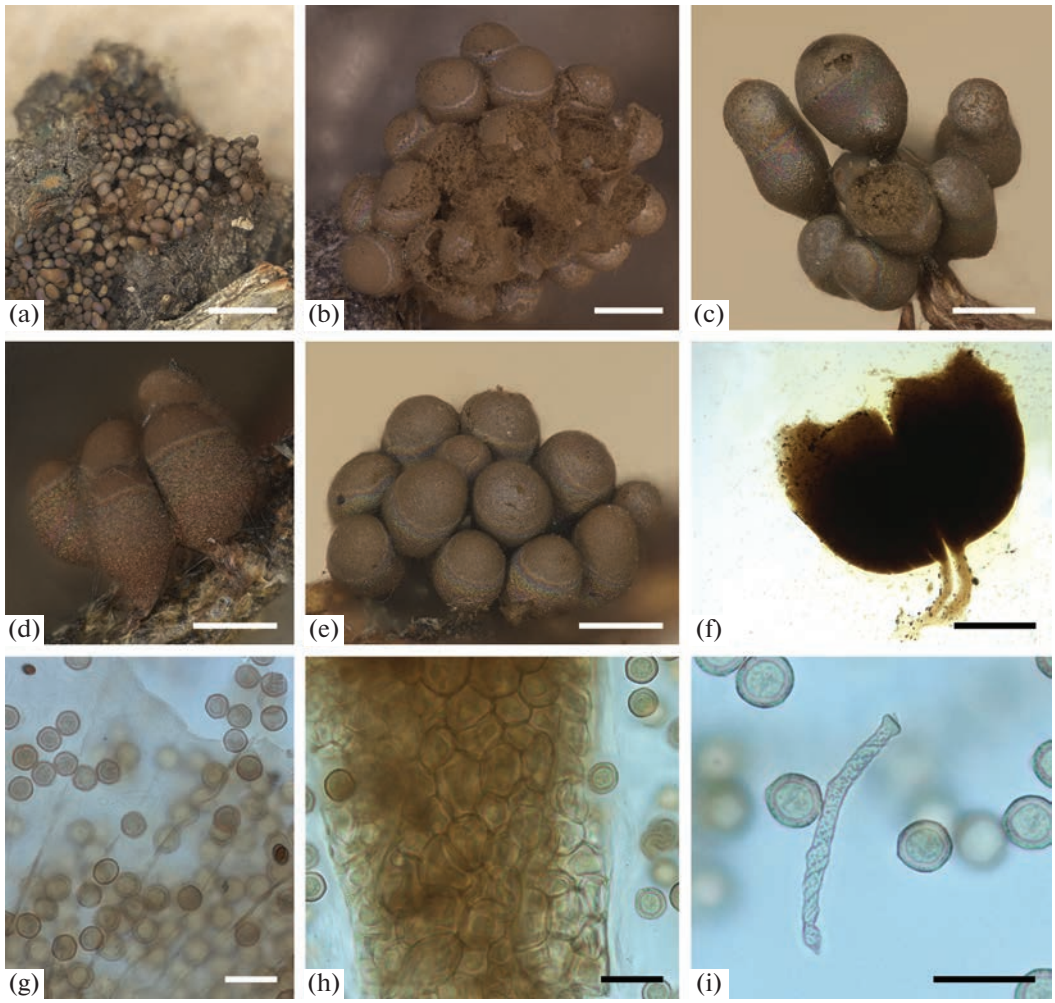

Fig. 2. *Arcyria brunneoiridescens*: a–f – sporangia (NSK 1031970, NSK 1031862, NSK 1016774, NSK 1016781, NSK 1030490, NSK 1016771), g – peridium and spores (NSK 1030490); h – spore-like bodies in the stalk (NSK 1030490); i – spores and capillitial thread (NSK 1030490). Scale – 2 mm (a), 0.5 mm (b–e), 200 μm (f), 20 μm (g–i).

have a different shape of endings within the same colony of sporangia: pointed or with a blunt ending up to 5 μm in diameter, or forked. Spore mass brown. Spores olive, light brown in transmitted light, verrucose, 8.6–11 μm diam. In SEM, spore ornamentation consists of large warts, between which small warts are scattered, sometimes the surface of the spore is covered only with large warts.

Type: United States, California, Modoc County, Canby, 1314 m, on cow dung, 17.09.1978, J.J. Cox, JJC 570 (holotype).

Specimens examined: Russia, Altai Territory, Zmeinogorsky District, Tigiretsky Ridge, stony screes, 51.0445° N, 82.9666° E, 1469 m, on dry dead leaves and at the base of lignified shoots of live *Goniolimon speciosum* (L.) Boiss., substrate samples coll. 29.06.2018, V.A. Vlasenko, moist chamber culture 12.01.2020, cult. and ident. A.V. Vlasenko, NSK 1016782; ibid., on dry dead leaves and at the base of lignified shoots of live *G. speciosum*, substrate samples coll. 29.06.2018, V.A. Vlasenko, moist chamber culture 14.02.2020, cult. and ident. A.V. Vlasenko, NSK 1016772, GenBank No: OR287437 (*18S nrDNA*); ibid., border of subalpine meadow and stony screes, 51.0441° N, 82.9670° E, 1462 m, on dry dead leaves and at the base of lignified shoots of live *G. speciosum*, substrate samples coll. 29.06.2018, V.A. Vlasenko, moist chamber culture 24.04.2020, cult. and ident. A.V. Vlasenko, NSK 1016773, GenBank No: OR287442 (*18S nrDNA*); ibid., on dry dead leaves and at the base of lignified shoots of live *G. speciosum*, substrate samples coll. 29.06.2018, V.A. Vlasenko, moist chamber culture 20.06.2020, cult. and ident. A.V. Vlasenko, NSK 1030490, GenBank No: OR287438 (*18S nrDNA*); Kuryinsky District, 51.7763° N, 82.3311° E, 348 m, on dry dead leaves and at the base of lignified shoots of live *Rumex confertus* Willd., substrate samples coll. 12.07.2015, V.A. Vlasenko, moist chamber culture 29.09.2021, cult. and ident. A.V. Vlasenko, NSK 1016771, GenBank No: OR287440 (*18S nrDNA*); Republic of Tyva, Kyzylsky district, 26 km northeast of the village of Cherby, 51.9252° N, 94.9766° E, 1092 m, valley dark coniferous forest, on the bark of live *Picea obovata* Ledeb., substrate samples coll. 10.08.2020, A.V. Vlasenko, moist chamber culture 15.01.2021, cult. and ident. A.V. Vlasenko, NSK 1016774, GenBank No: OR287441 (*18S nrDNA*); ibid., Tandinsky

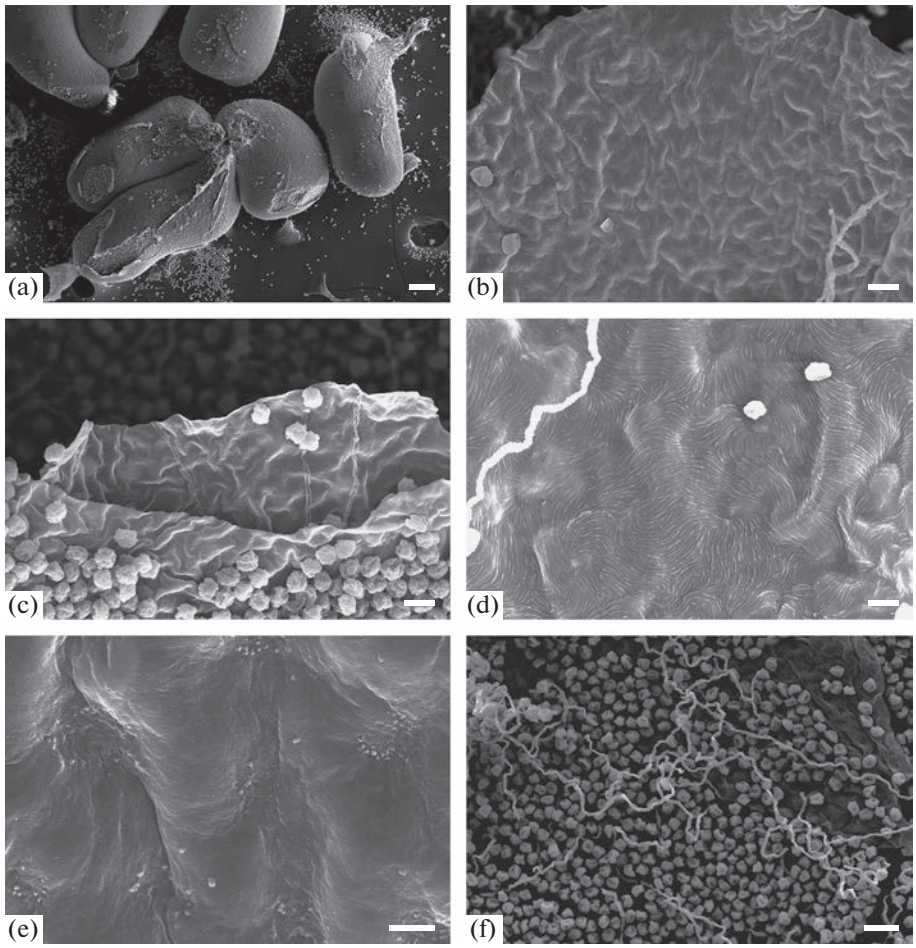

Fig. 3. *Arcyria brunneoiridescens* (SEM): a – sporangia (NSK 1016774); b – inner surface of peridium, capillitial threads, spores (NSK 1016774); c – inner surface of peridium, spores (NSK 1016781); d – inner surface of peridium, capillitial threads, spores (NSK 1016771); e – inner surface of peridium (NSK 1016774); f – capillitial threads, spores (NSK 1030490). Scale – 100 μm (a), 20 μm (f), 10 μm (b–d), 2 μm (e).

district, Yenisei highway, 50.8715° N, 95.1988° E, 953 m, light coniferous forest, on the bark of live *Larix sibirica* Ledeb., substrate samples coll. 12.07.2021, A.V. Vlasenko, moist chamber culture 13.01.2022, cult. and ident. A.V. Vlasenko, NSK 1031952; NSK 1031862, GenBank No: OR287441 (OR287439); NSK 1016791; ibid., on the bark of live *L. sibirica*, substrate samples coll. 12.07.2021, A.V. Vlasenko, moist chamber culture 18.01.2022, cult. and ident. A.V. Vlasenko, NSK 1031977; ibid., on the bark of live *Betula pendula* Roth, substrate samples coll. 12.07.2021, A.V. Vlasenko, moist chamber culture 18.01.2022, cult. and ident. A.V. Vlasenko, NSK 1031960, NSK 1031970; Republic of Sakha (Yakutia), near city of Yakutsk, larch forest, on the bark of live *Larix gmelinii* (Rupr.) Kuzen., moist chamber culture 13.01.2022, cult. and ident. A.V. Vlasenko, NSK 1016781.

DISCUSSION

According to the original description, *Trichia brunnea* is characterized by brown sporangia on stalks or sessile on restricted base, clustered in small groups, the peridium single, membranous, the capillitium elaters are smooth with spiral thickenings, with slightly swollen tips, the spores are olive, 10–11 mμ diam. with thick spore wall, ornamented with small warts.

Our specimens are presented by ovoid or irregular shape sporangia, which form crowded colonies with partial loss of individuality by individual sporangia and spiral ornamentation of capillitial threads resembles those of *Arcyria stipata* (Schwein.) Lister and *A. imperialis* Q. Wang et Yu Li.

A. imperialis originally described in the genus *Hemitrichia* as *Hemitrichia imperialis* G. Lister; later, was transferred to the genus *Arcyria* based on morphological features. Further, we confirmed in an *18S nrDNA* phylogeny that *Hemitrichia imperialis* should indeed be included in the genus *Arcyria* (Vlasenko et al., 2020).

Hollow transparent stalks filled with spore-like cells are a characteristic feature for members of the genus *Arcyria* (Poulain et al., 2011). In all our specimens of *Trichia brunnea*, spore-like cells are also present in the stalk. As for the spiral capillitial ornamentation, this morphological pattern appears not only in the genus *Trichia* but also in the phylogenetic clade of *Arcyria*

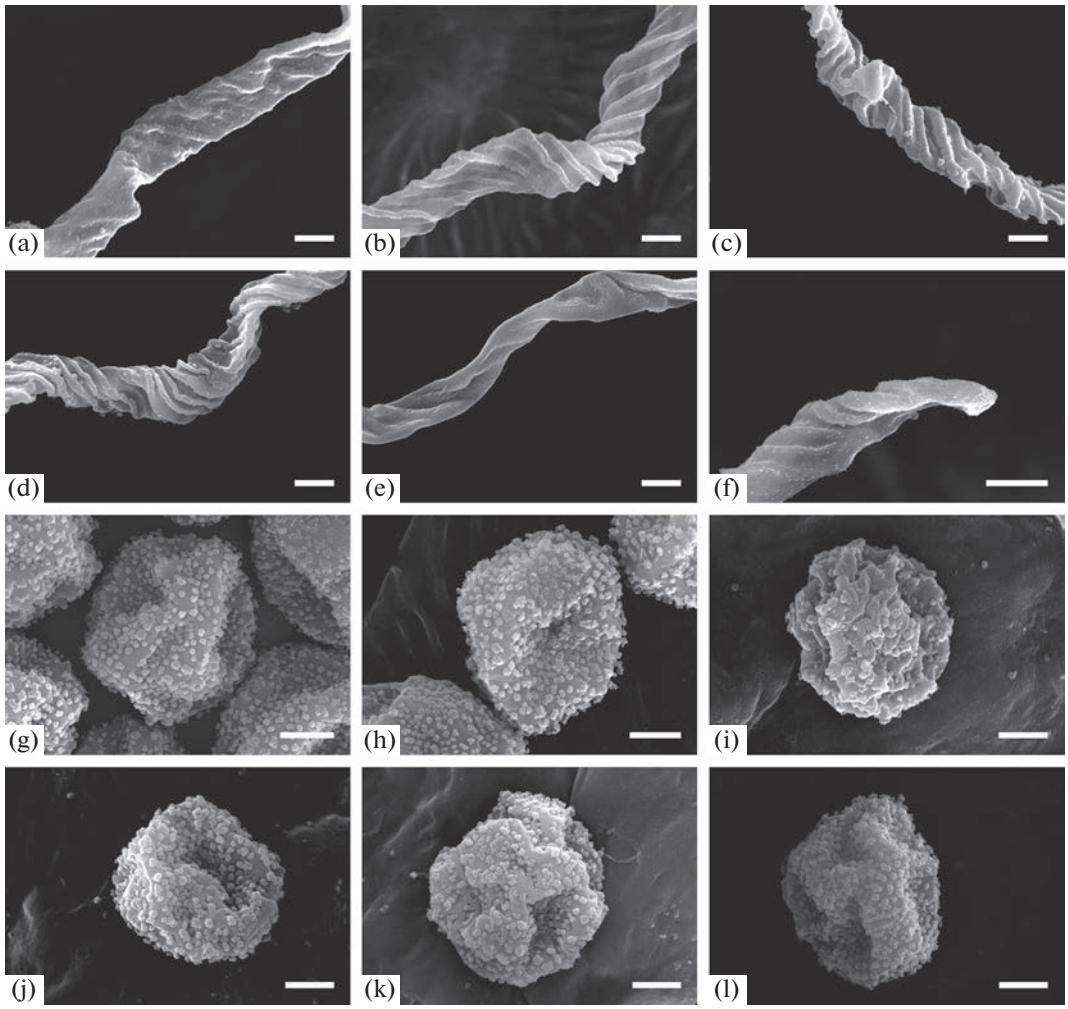

Fig. 4. *Arcyria brunneoiridescens* (SEM): a–f – capillitial threads (NSK 1016772, NSK 1016771, NSK 1016774, NSK 1016762, NSK 1016781, NSK 1016771); g–l – spores (NSK 1016772, NSK 1016771, NSK 1016781, NSK 1016762, NSK 1030490, NSK 1016774). Scale – 2 μm.

(e.g., *Hemitrichia leiocarpa*), in spite of the most of species of this clade lack spiral.

Previously, all known collections of *Trichia brunnea* were obtained in moist chamber cultures on weathered dung of herbivorous animals and this species was recognized as an obligate fimicolous (coprophilous) species (Eliasson, 2013). This conclusion is probably is connected with insufficiently studied ecology of this rare species.

This species has thick-walled spores. However, for our opinion, thick spore walls cannot be considered as an exclusive feature of fimicolous species. For example, specimens of *Arcyria globosa* collected in the Asian part of Russia always have a thick spore wall, while this species is common in epiphytic and litter substrate guilds in the arid regions of Siberia. (Vlasenko et al., 2021 a, b). It is possible that the thick spore wall is a morphological adaptation to survive in arid regions.

In this study we used a modified method of moist chamber cultures which allows us to record species that require a long period of incubation in moist chambers to form sporocarps. At the same time, excess water from the Petri dishes does not drain, the dishes are naturally ventilated, and the cultivation time increases to 3–6 months (Vlasenko et al., 2018). During 3 months, we found *T. brunnea* on different substrates collected in Siberia (Tyva and Yakutia) in period 2011–2022 years. In result, the species was registered on dung of animals (13 records), on plant litter (5 records), and even on tree bark birch, larch and spruce (8 records). Interestingly that sporocarps on the bark were obtained during 1.5 months, whereas on the droppings of herbivorous animals for 2.5–3 months. This shows a broader ecological niche for this species than previously thought.

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ment № 075-15-2021-1056 of September 28, 2021 between the BIN RAS and the Ministry of Science and Higher Education of the Russian Federation, also under Agreement № ЕП/29-10-21-4 of October 29, 2021 between BIN RAN and CSBG SB RAS. Samples of myxomycetes are deposited in M.G. Popov Herbarium, USU 440537, Novosibirsk.

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Филогения *Trichia brunnea* и новое название в роде *Arcyria* (*Trichiales*, *Myxomycetes*)

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Недавние филогенетические исследования указывают на таксономическую неопределенность некоторых видов рода *Arcyria* (*Arcyriaceae*) и *Trichia* (*Trichiaceae*). Например, филогенетическое положение *Trichia brunnea* до сих пор было не определено. Мы пересмотрели таксономическое положение этого вида на основе обширной выборки последовательностей 18S ярДНК, а также на морфологическом анализе спорокарпов и спор. Кратко представлена номенклатурная история *T. brunnea* и дано исчерпывающее морфологическое описание вида. В результате мы предлагаем перенос *T. brunnea* в род *Arcyria*. Название *Arcyria brunnea* уже существует, в связи с чем мы предлагаем новое название *A. brunneoiridescens* (= *Trichia brunnea*).

Ключевые слова: миксомицеты, распространение, таксономия, 18S ярДНК, *Amoebozoa*, *Arcyria*, *Myxogastria*, *Trichia*